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The "Pocosin" of Pike County, Alabama, and its bearing on certain problems of succession

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(WITH FOUR TEXT FIGURES)

In eastern North Carolina, where the geographical term "pocosin" is used more frequently than in all the rest of the world, it means a flat wet place with peaty soil, usually remote from large streams, with a scattered growth of trees, mostly *Pinus serotina*, and a dense shrubby undergrowth.* In South Carolina and Georgia this term is almost unknown,† but it reappears in the coastal plain of Alabama, with a very different meaning.

In a chapter contributed by E. Q. Thornton to Prof. Tuomey's second report on the geology of Alabama, published in 1858 (p. 244), we find the following interesting bit of information:

"East of this place [Troy] is a small scope of country of peculiar appearance, known as the Pocosson settlement. The vallies, which have the rank luxuriant growth of a swamp, are surrounded on three sides by a ridge of snow-white sand, which seems to have been heaped up by the tides on a sea-shore. The only occupant of the hills is a scrubby oak covered with long moss. The soil is exceedingly unproductive, and soon wears out by cultivation."

* See Bull. Torrey Club **34**: 361–363. 1907; C. A. Davis, N. C. Geol. Surv. Econ. Paper 15: 149–150. 1910; L. W. Stephenson, N. C. Geol. Surv. Vol. 3: 280. *pl. 24B*. 1913.

† Miss E. F. Andrews (see Torreya **13**: 64–66. 1913) wrote me early in 1913 that she had heard the term applied to certain "large flowery swamps" in the vicinity of Albany, Georgia, where she used to live; and the government soil survey of Dougherty County, Georgia, published in October, 1913, indicates a "Percosin Creek" a few miles west of Albany, but says nothing about any application of the name to vegetation. Still more recently (March, 1914) I have heard of an occurrence of the term in West Florida.

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In Dr. Eugene A. Smith's description of Pike County in his report on the agricultural features of Alabama (Tenth Census U. S. 6: 151; Geol. Surv. Ala., Report for 1881 and 1882, p. 522. 1884) these observations of Thornton's are briefly referred to. About the same time, in the 9th volume of the Tenth Census (p. 528), Dr. Charles Mohr published some more definite information about the vegetation of the same place, as follows:

"PIKE COUNTY.—On the broad ridges which form the divide between the waters of the Pea and Conecuh rivers, upon a purely sandy soil, are found, within the forest of long-leaved pine, tracts with strictly-defined outlines from a half mile to several miles in width, covered with a dense vegetation of small trees and shrubs peculiar to the perpetually moist and cool hummocks* of the coast. The soil covered with this growth presents no unusual features; it is as poor and arid as that covering the rest of these heights. Surrounded on all sides by pine forests, not a single pine tree is seen within the limits of these glades, called by the inhabitants 'pogosines,' an Indian name the meaning of which I was unable to learn.

"The trees are of small growth, the willow oak, the water oak, beech, red maple, and black gum rarely rising to a height of more than 30 feet among the sourwoods, junipers, hornbeams, hollies, papaws, fringe trees, red bays, and other trees of the coast. These glades verge upon deep ravines from which issue large springs, and from this fact I conclude that, below their sandy, porous soil, strata must exist perpetually moistened by subterranean waters near enough to the surface to supply the moisture necessary to support such a luxuriant vegetation."

There seems to be no reference to this interesting place in Dr. Smith's report on the geology of the coastal plain of Alabama (1895), or in Dr. Mohr's Plant Life of Alabama (1901). In the summer of 1906 Dr. Smith and the writer were in Pike County together for a short time, and heard some accounts of the "pocosin," which led Dr. Smith to make his first visit to it a little later.

In 1910 a soil survey of Pike County was made by W. E. Tharp, of the U. S. Department of Agriculture, and W. L. Lett and W. E. Wilkinson, representing the State; and on the map accompanying their report, published in December, 1911, the location of the pocosin is shown, probably for the first time, but there is not a word about it in the text. Stranger still, its soil is not differentiated on the map from that of the surrounding country ("Norfolk coarse sand"), although it does differ in at least one important particular.

* Dr. Mohr doubtless wrote "hammocks," as he did in his Plant Life of Alabama 17 years later, but it was evidently changed to "hummocks" in Washington, as it was throughout the 5th and 6th volumes of the same series, except on the maps, and one or two places in the text that escaped the proof-readers. (See Geol. Surv. Ala. Monog. 8: 83. 1913.)

Guided by the map just mentioned, the writer visited the spot on November 6, 1912, and March 27, 1913, and made a rough quantitative study of its vegetation. An incessant rain at the time of the first visit interfered somewhat with note-taking and made photography out of the question, but conditions were more satisfactory the second time, when the views here published were taken. A brief mention of it, with the only photograph of its vegetation hitherto published, appeared last summer in my report on the forests of Alabama.*

The so-called pocosin (Dr. Mohr's description above quoted implies the existence of several such areas, but I know of only one) embraces a hundred acres or more, mostly in Section 7, T. 9 N., R. 22 E., in the midst of a few square miles of undulating sandy country on the east side of Walnut Creek, about half way between Troy and Brundidge, and about 50 miles south of the fall-line and 100 miles from the Gulf coast. The pocosin itself is practically untouched by civilization, except for having one or two little-used roads through it, but the surrounding sandy country is partly under cultivation. As observed by Thornton, however, the sand is much less productive than the loamy soils which prevail elsewhere in Pike County and other parts of the southern red hills or Eocene region of the coastal plain. Where not cultivated it bears a vegetation much like that of the sand-hills of Georgia,† but the soil is evidently a little richer in mineral plant food than that of the average sand-hill, as shown by the prevalence of *Pinus echinata* and the scarcity of *Pinus palustris*.‡

In the following list of sand-hill plants growing around the pocosin the trees, shrubs and herbs are arranged as nearly as possible in order of abundance, but the data are not sufficient for assigning percentages to them. Evergreens are indicated by heavy type.

TREES

Pinus echinata	Hicoria glabra
Crataegus Michauxii?	Quercus stellata
Quercus Catesbaei	Quercus marylandica
Quercus cinerea	Nyssa sylvatica
Quercus Margaretta	**Pinus palustris**

* Geol. Surv. Ala. Monog. 8: 99–100, 160–161. June, 1913.

† See Ann. N. Y. Acad. Sci. 17: 82–89. 1906.

‡ This is in a narrow belt of the coastal plain where the long-leaf pine is very rare. See Geol. Surv. Ala. Monog. 8: 99. 1913.

SHRUBS AND VINES

Batodendron arboreum
Ceanothus americanus
Gaylussacia dumosa
Asimina parviflora
Osmanthus americana
Chionanthus virginica
Gelsemium sempervirens

HERBS

Opuntia vulgaris
Pteridium aquilinum
Afzelia pectinata
Kuhnistera pinnata*
Solidago odora
Stenophyllus ciliatifolius*
Polypodium polypodioides
Iris verna
Triplasis americana*
Ionactis linariifolius
Cracca virginiana
Chrysopsis aspera?
Coreopsis major Oemleri
Tillandsia usneoides
Sorghastrum secundum†
Siphonychia sp.
Pitcheria galactioides*
Astragalus villosus*
Warea cuneifolia‡

LICHENS

Cladonia sp.

This vegetation, like that on typical sand-hills, is not very dense, as shown by one of the accompanying illustrations (FIG. 1). Apparently about one third of the woody plants (counting individuals, not species) are evergreen.

The pocosin itself seems to center around the precipitous heads of a few small tributaries of Walnut Creek, but its vegetation, except in the bottoms of the ravines, is not at all of a swamp character, the statements of Thornton and Mohr to the contrary notwithstanding. Its soil was doubtless originally the same as that of the surrounding sandy country, but it is now covered and more or less mixed with a thin layer of humus, derived from the trees and protected from desiccation and oxidation by their shade, as in other dense forests the world over. In this forest there is a characteristic faint odor of sour humus (corresponding approximately with the raw humus of Warming§ or more closely with the upland peat of Coville‖), as in the mountains of North Carolina

* These five species do not seem to have been found so far inland in Alabama before. Three of them are Leguminosae.

† Apparently not previously reported from Alabama. (See Ann. N. Y. Acad. Sci. 17: 300. 1906.) But in September, 1912, I found it in considerable abundance in the pine-barrens of Clarke, Monroe and Baldwin Counties.

‡ Another addition to the Alabama flora, its previously known range being from South Carolina to Florida.

§ Oecology of Plants, 62–63. 1909.

‖ U. S. Dept. Agr. Bur. Plant Industry Bull. 193: 32–34. F 1911; Jour. Wash. Acad. Sci. 3: 84–86. F 1913.

and many other places where humus accumulates on a soil that is poor in animal life or not intrinsically very fertile. The boundary between the pocosin and sand-hill vegetation is not very sharp, but it is comparatively easy to fix it definitely enough for statistical purposes. In attempting to make a quantitative analysis of the vegetation, however, one encounters a difficulty in that it is a many-storied forest, in which there seem to be all gradations in

FIG. 1. Sand-hill vegetation near the pocosin, with *Pinus echinata*, *Quercus Catesbaei*, *Crataegus*, *Batodendron*, etc.

size between large trees and shrubs, and it is not exactly right to include both trees and shrubs in the same list for the purpose of calculating percentages. The following list is divided into more classes than usual, and the relative position of the species within each class is approximately correct, but it gives no idea of the relative abundance of species in different classes. The illustrations, however, partly make up for this. (FIGS. 3, 4.)

LARGE TREES

Quercus laurifolia
Hicoria glabra?
Tilia heterophylla?
Magnolia grandiflora
Fagus grandifolia
Quercus alba
Prunus serotina
Fraxinus americana?
Quercus velutina

SMALL TREES

Osmanthus americana
Persea Borbonia
Quercus sp.*
Ostrya Virginiana
Batodendron arboreum
Cornus florida
Viburnum rufidulum
Prunus caroliniana
Crataegus sp.
Acer floridanum
Prunus umbellata?
Bumelia lanuginosa
Crataegus Michauxii? (toward edges)
Quercus Margaretta (toward edges)
Cercis canadensis
Oxydendron arboreum
Ilex opaca
Amelanchier sp.

SHRUBS

Hamamelis virginiana
Chionanthus virginica
Sebastiana ligustrina
Aralia spinosa
Callicarpa americana
Aesculus Pavia
Kalmia latifolia

WOODY VINES

Vitis rotundifolia
Bignonia crucigera
Rhus radicans

HERBACEOUS VINES

Smilax pumila
Mitchella repens
Dioscorea sp.

ORDINARY HERBS

Trillium Hugeri
Asarum arifolium
Galium uniflorum
Polygonatum biflorum
Solidago odora (toward edges)
Monotropa uniflora
Panicum sp.
Viola sp.
Sanicula sp.
Dasystoma quercifolia
Carex floridana
Opuntia vulgaris
Conopholis americana

EPIPHYTES

Polypodium polypodioides
Tillandsia usneoides

BRYOPHYTES AND THALLOPHYTES

Thuidium sp.
Clavaria sp.

It is interesting to note that among 57 species here listed as growing in the pocosin there is only one fern, and such large families as Gramineae, Cyperaceae, Leguminosae and Com-

* An unidentified—and probably undescribed—oak, somewhat similar in appearance to *Q. marylandica* Muench. and *Q. arkansana* Sarg., but apparently more closely related to *Q. nigra* L. (*Q. aquatica* Walt.), *Q. myrtifolia* Willd. (as that species is commonly interpreted), and *Q. microcarya* Small. I have never seen anything like it elsewhere. It grows mostly toward the edges of the pocosin, but not in the sandhill vegetation. It is one of the commoner species there, as indicated by its position in the list, and it is difficult to understand how Dr. Mohr overlooked it if he visited this same spot, unless he was there only in winter, when it was leafless. (FIG. 3.)

positae are also represented by only one species each. There are five oaks (the same number as in the surrounding sand-hill area) three representatives of the Ericales, and three colorless saprophytes or root-parasites, namely, *Monotropa*, *Conopholis* and *Clavaria*.

Although there are no quantitative figures to show it, just about half of this vegetation is evergreen. It is very similar to

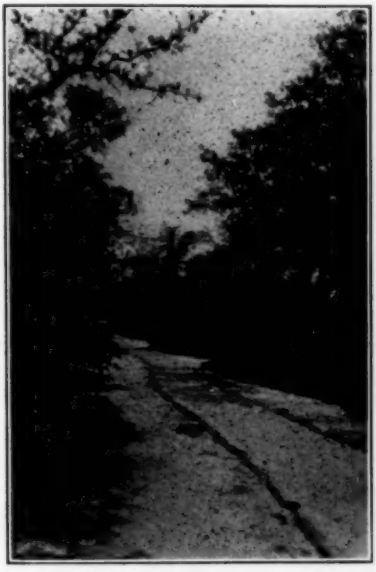

FIG. 2

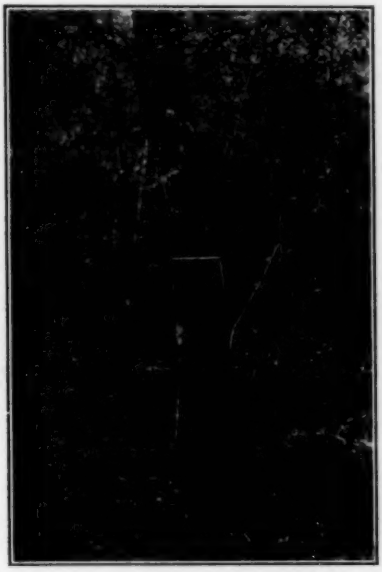

FIG. 3

FIG. 2. Scene on sandy road just outside of the pocosin. Flowering branches of *Quercus stellata* in upper left corner; *Quercus Catesbaei* at right, bearing many dead leaves of the preceding season.

FIG. 3. Trunk of the undescribed *Quercus* (34 inches in circumference, breast-high, and about 30 feet tall) in the pocosin near its eastern edge.

that of some of the sandy hammocks of Georgia and Florida;* and it may be more or less of an accident that the name *pocosin* was applied to this place by the early settlers instead of *hammock*.†

* See Ann. N. Y. Acad. Sci. **17**: 98–102. 1906; Bull. Torrey Club **38**: 515–517. 1911.

† If the early immigrants had come from the southeastward instead of northeastward they would doubtless have been familiar with hammocks, which are more prevalent nearer the coast.

The proportion of evergreens is usually somewhat larger in the hammocks nearer the coast, however. The more remote relationships of this vegetation may be indicated by saying that it is intermediate in character between the deciduous forests that are common on rich uplands in the moderately humid parts of the North Temperate zone, and the "sclerophyllous forests" of Warming and other European ecologists.

A list of the characteristic plants of the ravines will complete the description of the pocosin vegetation. They are about as follows (the arrangement being the same as in the two preceding lists):

TREES

Osmanthus americana
Magnolia grandiflora
Ilex opaca
Liriodendron Tulipifera
Magnolia glauca
Cornus florida
Symplocos tinctoria
Hicoria alba
Fagus grandifolia

SHRUBS

Kalmia latifolia
Ilex coriacea

HERBS

Asarum arifolium
Smilax pumila

MOSSES

Thuidium sp.

Evergreens are decidedly in the majority here.

Previous visitors to this place have been more or less mystified by the occurrence of such luxuriant vegetation in such sandy soil. The explanation is doubtless the same as for other sandy hammocks, and is very simple to one familiar with conditions in South Georgia and Florida.

The pocosin area, exclusive of the ravines, was presumably at some time in the past covered with the same sort of sand-hill vegetation that now partly surrounds it. Vegetation of a denser, more "climactic"* type must have gradually spread from the creek valley up the ravines to their heads, and then out across the

* This adjective, derived from *climax*, is rarely if ever seen in botanical literature, but some such word seems to be needed. Some ecologists have been using *climatic*, an entirely different word, to convey essentially the meaning here intended; while many use *climax* and *mesophytic* more or less interchangeably, which seems to be a perversion of the original meaning of the latter.

sand, making more humus all the time, and crowding out the intolerant sand-hill plants, as in normal succession the world over; and it is probably still spreading slowly but surely. The pocosin vegetation is simply the climax for that type of soil, while the sand-hill vegetation is the pioneer.

In explaining this succession there is one environmental factor that must not be lost sight of. Most of the plants in the pocosin,

FIG. 4. Typical pocosin vegetation. *Magnolia grandiflora* (the largest trunk), *Osmanthus*, *Batodendron*, *Prunus caroliniana*, etc. Ground covered with undecayed leaves.

as in other hammocks, are very sensitive to fire. Fire often sweeps through the upland pine-oak-hickory woods that are common on the better soils of the same region, but the sand-hill vegetation is ordinarily too sparse and open to carry a ground fire any distance, so that it protects the pocosin vegetation on three sides from any fires which may originate in the surrounding country. Protection on the remaining side is afforded by the swamps and bottoms of Walnut Creek, or the broken topography. The hammocks of the Altamaha Grit region of Georgia are similarly protected from fire by the creek swamp on one side of them and the sand-hills on the other, and this protection has been an essential factor in determining their present vegetation.*

Finally this Alabama pocosin throws valuable light on the

* See Bull. Torrey Club 38: 524–525. 1911.

relation of evergreens to soil and succession. Although a great deal has been written about the phenomena of succession in various parts of the world, no one yet seems to have published any satisfactory short definition of pioneer and climax vegetation by which they may be recognized wherever found, without knowing the species; and consequently every ecologist has his own views on these points, and perhaps no two of them agree exactly. It is probably pretty generally agreed that normal succession (biotic succession of Cowles*) involves enrichment of the soil in some way; and as evergreens, in temperate climates at least, are well known to be most abundant in the poorer soils,† I supposed until about two years ago that no typical climax forest could contain any evergreens; and that view has found expression in my writings. Closely connected with that belief was one which seems to be still very generally held, namely, that for every (climatic) *region* there is *one* climax type of vegetation toward which all others are tending. I am now pretty well satisfied, however, that almost every type of *soil* has its own characteristic pioneer and climax vegetation, more or less distinct from those of other types.

The proportion of evergreens in a given habitat or region seems to be correlated with the amount of available potash (and perhaps other minerals) in the soil,‡ and therefore should not be affected much by the sort of succession whose essential feature is the accumulation of humus, or the progress of nitrification. Although an admixture of humus is indeed believed to increase the availability of the mineral plant foods in soil, a soil totally lacking in potash or lime would gain none of these ingredients from humus formed in place. It is even possible that in soils deficient in soluble minerals—as is the case with most sandy and peaty soils—and protected from fire like our pocosin, a considerable proportion of the potash within reach of the roots of trees is locked up for several years at a time in the dead leaves which lie on the ground undecayed, and thus the proportion of evergreens may actually increase with succession, as it does in the present case, where the ravines have the most evergreens and the sand-hills the fewest.

* Bot. Gaz. **51**: 171–180. 1911; Ann. Assoc. Am. Geogrs. **1**: 12–19. 1912.

† See Rep. Mich. Acad. Sci. **15**: 197. 1914.

‡ See Geol. Surv. Ala. Monog. 8: 28–29; Torreya **13**: 140, 141, 143; Bull. Torrey Club **40**: 398. 1913.

(In the pine-barrens frequent fires return the potash, etc., quickly to the soil, while in calcareous or clayey soils there are usually many earthworms, centipedes, snails, bacteria or other soil organisms which assist greatly in converting the leaves into humus.*) Another successional factor which doubtless tends to diminish the availability of mineral nutrients in the soil is the denser shade of the climax vegetation; for this lowers the temperature of the soil in summer and probably makes the ground-water level more constant, besides diminishing evaporation and eremacausis.

Although no chemical analysis of the pocosin soil has been made, it is evident from a casual inspection that it consists mostly of siliceous sand, and must be rather poor in soluble minerals, like the sandy hammocks of Florida. The climax vegetation of the more clayey soils in the same region is found on river-banks, bluffs, and sides of ravines, where fire is kept away pretty well by the topography; and it differs considerably from that of the pocosin. The following list, of trees only, is a generalized one for the upland climax forests of the whole southern red hill region of Alabama. The species are arranged approximately in order of abundance, as before.

Liquidambar Styraciflua
Pinus Taeda
Liriodendron Tulipifera
Fagus grandifolia
Quercus alba
Cornus florida
Magnolia grandiflora
Pinus glabra
Hicoria alba
Magnolia macrophylla
Ilex opaca
Nyssa sylvatica
Ostrya virginiana
Oxydendron arboreum
Acer floridanum
Fraxinus americana
Tilia heterophylla?
Quercus nigra
Cercis canadensis
Halesia diptera
Magnolia acuminata
Quercus rubra
Symplocos tinctoria
Magnolia pyramidata

Most of the species in this list are common also to the pocosin, but their relative abundance is different, and the proportion of evergreens is considerably less, being probably not over one third or one fourth. Evergreens naturally differ somewhat among themselves in their soil requirements, and it happens that the

* Mr. Coville's valuable paper on the formation of leaf-mold (Jour. Wash. Acad. Sci. **3**: 77–89. 1913) should be consulted in this connection.

two pines here listed prefer richer soils than all the other southern pines and some deciduous trees.

Although it is digressing a little from the scope of this paper, it is interesting to note that the hammocks and river-bluffs of the Altamaha Grit region of Georgia* differ from each other in much the same way that the pocosin does from the bluffs, etc., just mentioned. Both hammocks and river-bluffs are covered with climax forests, but the soil is sandy in one case and loamy in the other, which makes considerable difference in the vegetation. From the frequency numbers which have been published in the work cited, it appears that 79.6 per cent. of the trees and 30.5 per cent. of the shrubs in the hammocks are evergreen; while the corresponding figures for river-bluffs are 37 and 15; a difference whose significance was not suspected until long after these Georgia lists were published. The sand-hills which border the Georgia hammocks and protect them from fire have been estimated in the same way to have 28.2 per cent. of their trees and 48.3 per cent. of their shrubs evergreen.

SUMMARY

This so-called pocosin (which has little in common with the typical pocosins of North Carolina) is a many-storied climax forest of a type characteristic of dry sandy soils in the coastal plain of Alabama, Georgia, and northern Florida. The accumulation of humus—and consequently the development of climax vegetation—began in ravines, and has been favored by the protection from fire afforded by the sparseness of the surrounding pioneer vegetation.

Something like half of the woody plants of the pocosin are evergreen, which is evidently a larger proportion of evergreens than in the case of the pioneer vegetation of the same soil and of the climax vegetation of soils richer in mineral plant food in the same region and elsewhere.

Each fundamentally different type of soil seems to have its own characteristic pioneer and climax vegetation; and the proportion of evergreens in this case—if not in many others—increases with normal succession, owing probably to the lowering of soil temperatures during the growing season, and to the locking up of plant food in undecayed leaves or sour humus, among other things.

* Ann. N. Y. Acad. Sci. 17: 98–109. 1906.

Seed development in the genus Peperomia*

G. Clyde Fisher

(with plates 3–6 and a text figure)

[*Concluded from page 156*]

General Discussion

Whether the sixteen-nucleate embryo sac of *Peperomia* is to be regarded as primitive, depends upon the homologies assumed or proved for the various structures found in this unusual type of embryo sac. In view of this, and since no axial row of megaspores is formed, the first question that naturally arises is whether the first four nuclei in the embryo sac are the morphological equivalents of four megaspore nuclei.

It is quite generally agreed that the cells of the axial row in the nucellus formed by the division of the definitive archesporial cell in most Angiosperms are homologous with those having a similar development in Gymnosperms; in both cases they are almost universally known as megaspores. There exists a further homology, although not quite so close, between the megaspores of Angiosperms and Gymnosperms and those of the heterosporous Pteridophytes. The tetrads of microspores, also, in all of these groups are homologous with one another, and, in a slightly different degree, with the megaspores in the same group. The evidence for these views has been well presented by Strasburger (**73, 75**), Overton (**55, 56**), Juel (**36**), Körnicke (**40**), Coulter (**13**), and others.

That the first four nuclei in the embryo sac of *Peperomia* are homologous with megaspore nuclei seems equally clear. The following facts indicate the correctness of this conception:

(1) The cell, the nucleus of which gives rise to these first four nuclei, may be considered, without valid objection, a megaspore mother-cell. It is developed in the position of the axial row. It is derived from a single primary archesporial cell, which cuts off

* Botanical Contribution from The Johns Hopkins University, No. 35.

a single tapetal cell. In fact, its position and whole antecedent development, being so closely similar to that so generally found in Angiosperms, constitute a strong bit of positive evidence for the view that it is a megaspore mother-cell.

(2) As is evidenced by the occurrence of synapsis in the nucleus of the definitive archesporial cell, preceding its division, the two divisions by which these four nuclei are formed are the reduction divisions, as is the case in the last two divisions in the formation of the megaspore nuclei in all other plants in which they are formed —so far as they have been investigated. In rare cases like that of *Alchemilla speciosa* (Murbeck, **53, 54**; Strasburger, **74**), in which apparent megaspore-formation occurs without reduction of chromosomes, there is no sexual fusion in the initiation of the embryo which is later developed in the embryo sac. Therefore, as Strasburger contends, such abnormal cases can not be considered examples of true megaspore-formation. The presence of the reduction divisions is considered by some workers as sufficient evidence for the acceptance of the theory of the homology of the megaspores of Angiosperms with those of the Gymnosperms and the higher Pteridophytes. It should mean as much in *Peperomia* as it does elsewhere in heterosporous plants.

(3) The tetrahedral arrangement of these first four nuclei points more strongly to the homology in question than does the linear tetrad, or axial row, arrangement, which occurs in nearly all seed-plants, both Gymnosperms and Angiosperms—since a tetrahedral arrangement of the microspores is found in nearly all heterosporous plants and in the megaspores of all heterosporous Pteridophytes. The linear tetrad of megaspores is universal in the Cycadales, the Coniferales, and the Ginkgoales, in all investigated cases known to the writer; but Juel (**36**) found a close approach to the tetrahedral arrangement in the megaspores of *Larix sibirica* as a general rule, the typical axial row being seldom found. The tetrahedral arrangement of megaspores is not altogether unknown in Angiosperms, having been observed in *Fatsia japonica* by Ducamp (**17**). Transitions between the axial row and the tetrahedral arrangement have been observed in *Aralia racemosa* by Ducamp (**17**), in *Garcinia* by Treub (**77**), in *Burmannia Championii* by Ernst and Bernard (**22**), in *Cynomorium*

by Juel (37), and in *Smilacina stellata* by McAllister (45). The case of *Smilacina* is particularly interesting here since the four megaspores show various transitions between the typical axial row and the tetrahedral arrangement. Moreover, after the megaspores are formed and unmistakably separated by walls, the walls disappear. The megaspore nuclei now become the first four nuclei of the embryo sac, and at this stage they assume the tetrahedral arrangement very similar to that in the four-nucleate embryo sac of *Peperomia*. It is not only in *Peperomia* that the first four nuclei of the embryo sac are arranged tetrahedrally, but this is likewise true in all genera in which sixteen free nuclei are formed in the embryo sac—namely, in *Gunnera* (Schnegg, 64; Ernst, 20, 21; Modilewski, 48; Samuels, 59), in *Sarcocolla* (Stephens, 70), in *Brachysiphon* (Stephens, 70), in *Penaea* (Stephens, 70), and in *Euphorbia* (Modilewski, 49, 51, 52).

(4) The fact that the tetrad is always complete in number of nuclei in *Peperomia* makes the homology seem rather more probable in this genus than it is in plants in which the axial row is incomplete, as for example, in one consisting of three cells instead of four.

(5) Eleven species of *Peperomia* have been shown to have sixteen nuclei in the mature embryo sac. In addition to the six here investigated are: *P. pellucida* (Campbell, 6), *P. hispidula* (Johnson, 34), *P. Sintenisii*, *P. arifolia*, and *P. Ottoniana* (Brown, 4). No species has been found to have any other number. As Brown (4) points out, the presence, in the mature embryo sac of *Peperomia*, of the larger number of nuclei than in the sac of ordinary Angiosperms, is in harmony with the view that more megaspore nuclei are concerned in the formation of the *Peperomia* type of embryo sac.

(6) The fact that all four nuclei divide, or germinate, can not militate against the theory that they are homologous with megaspore nuclei, because there are cases in which megaspores are undoubtedly formed and in which they all germinate—that is, the nuclei all divide. This is true, for example, in *Crucianella* (Lloyd, 41), in *Smilacina stellata* (McAllister, 45), and sometimes in *Epipactis* (Brown & Sharp, 5). And then there are intermediate cases in which one or more of the non-functional mega-

spore nuclei divide, e. g. in *Cercis Siliquastrum*, *Phaseolus multiflorus*, and *Erythrina Crista-galli*—all three investigated by Guignard (**24**). Another interesting case of this kind was found in *Scilla* (McKenney, **46**).

(7) That all four nuclei take part in the formation of one embryo sac can not constitute a valid objection to the view, because there are cases where megaspores are undoubtedly formed and in which all four participate in the formation of one embryo sac, as in *Smilacina stellata* (McAllister, **45**), and sometimes in *Epipactis* (Brown & Sharp, **5**), the walls following the first two divisions of the megaspore mother-cell being evanescent in both cases. In the former case the megaspores are frequently arranged in an axial row, but as was mentioned above, the arrangement is very often an intermediate condition between the axial row and the tetrahedral arrangement, while in *Epipactis* the megaspores always have the linear arrangement.

In *Euphorbia procera* and *E. palustris* (Modilewski, **49, 52**) and in the Penaeaceae (Stephens, **70**), the quadripolar grouping of the nuclei in the mature embryo sac furnishes a strong bit of evidence that the embryo sac in each of these cases is a composite structure derived from the equivalents of four megaspore nuclei. The same may be true of *Peperomia*, which has the same number of nuclei in the mature embryo sac, even though the nuclei do not have the quadripolar grouping.

(8) Another significant piece of evidence is that there is a resting period following the second division in the embryo sac—that is, following the four-nucleate stage. This was observed in every species of *Peperomia* which was sufficiently studied. As is well known, a resting stage following the formation of the four megaspores is almost universal in plants. So, this phenomenon is in harmony with what would be expected.

(9) One of the strongest pieces of evidence favoring this view is the appearance of evanescent walls following the first and second divisions in the embryo sac of *Peperomia*—together with the fact that these walls have never been seen in the eight-nucleate embryo sac—that is, following the third division. These walls were first reported by Brown (**4**) in *Peperomia Sintenisii* and in *P. arifolia*. They have been seen by the writer in seven other

species of *Peperomia*, namely: *P. reflexa*, *P. verticillata*, *P. scandens*, *P. Fraseri* var. *resediflora*, *P. blanda*, *P. galioides*, and *P. Langsdorffii*(?). Similar evanescent separating walls occur in *Smilacina stellata* (McAllister, **45**) and in *Epipactis* (Brown & Sharp, **5**), in which cases it is plain that they are megaspore walls. Wiegand (79) reports an evanescent wall between the first two nuclei in the embryo sac of *Convallaria*, in which case there are no degenerating megaspores, but the definitive archesporial cell forms the embryo sac directly, and this wall very probably represents a megaspore wall. In this case, however, only the heterotypic division is followed by an evanescent wall.

The appearance of separating walls is, however, not absolutely essential in the formation of megaspores in cases where it is generally admitted that megaspores occur, *e. g.* the walls usually do not appear in *Crucianella* (Lloyd, **41**), or in *Asperula* (Lloyd, **41**), and sometimes not in *Eichhornia* (Smith, **68**) or *Avena* (Cannon, **10**). In each of these cases, however, the embryo sac develops from a single megaspore nucleus, while the others degenerate, regardless of the absence of walls. But, since separating walls do generally appear between the megaspore nuclei in other plants, their presence in *Peperomia* certainly strongly favors the homology.

Another explanation of the occurrence of these walls, in harmony with Campbell's (**7**) view, was suggested by Brown (**4**) and immediately rejected. He says: "If the walls corresponded to those of prothallial cells, we should expect to find them in the third division, but here not even a cell-plate was seen. Besides this, the nearest phylogenetic relatives in which the first divisions of a megaspore result in a cellular structure are found among the leptosporangiate Filicales, where the heterospory is supposed to be of rather late origin, and it does not seem probable that *Peperomia* has reverted to the characters of an ancestor as remote as one in which we would find the first divisions of the megaspore giving rise to a cellular structure."

Since the separating walls occur in *Peperomia* following the first and second divisions only, in the embryo sac, and not after the third division, it is difficult if not impossible to conceive of any satisfactory homology for them, except that with the mega-

spore walls of other Angiosperms, that is, if it be admitted, as it is so generally, that megaspores occur in Angiosperms.

From these significant relations—from the origin of the embryo sac from what seems clearly a megaspore mother-cell, from the occurrence of the reduction division of its nucleus, from the tetrahedral arrangement of the first four nuclei, from the complete number in the tetrad, from the resting period following the formation of the tetrad, from the increased number of nuclei in the sac, and from the appearance of evanescent walls—from all these facts in favor of our view, together with the fact that the germination of all four megaspores and the participation of all of them in the formation of one embryo sac do not constitute valid objections to the theory, we are very strongly inclined to the view that the first four nuclei in the embryo sac of *Peperomia* are the equivalents of megaspore nuclei.

This theory of homologies is in harmony with the classifications of embryo sacs by recent workers (Ernst, **20**; Coulter, **13**; Samuels, **59**) with regard to the number of generations of nuclei from the beginning of the reduction division to the mature sac.

TEXT FIG. 1 illustrates diagrammatically the known types of derivation of the mature embryo sac from the definitive archesporial cell. The order in which these are arranged will suggest the phylogenetic sequence in which certain chief steps in the reduction of the number of cells or nuclear divisions between the definitive archesporial cell and the mature sac may have occurred. It also indicates the number of degenerating megaspores formed, where any occur.

In the type illustrated by TEXT FIG. 1*a*, there are *five* cell- and nuclear generations (the first two being cell-generations, and the last three being nuclear generations) in the development from the definitive archesporial cell to the mature embryo sac, which latter is of the common eight-nucleate type. The embryo sac is here indisputably the product of one megaspore, which divides three times.

In the type illustrated by TEXT FIG. 1*b*, the case is similar to that in TEXT FIG. 1*a*, but the upper cell formed by the first division of the definitive archesporial cell does not divide further. The embryo sac here contains eight nuclei, and is again clearly the
roduct of but one megaspore, which divides three times.
p

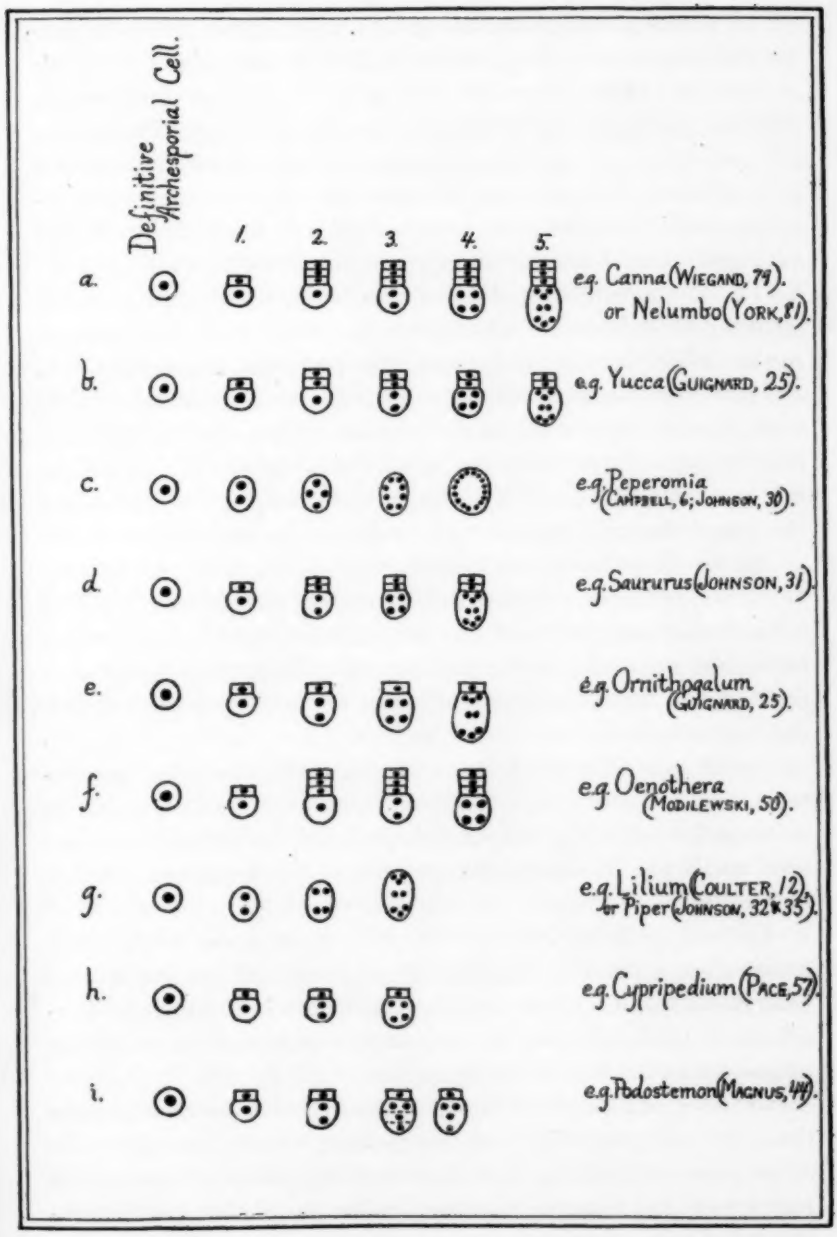

FIG. 1. Diagram illustrating the various types of embryo-sac development.

In the type illustrated by TEXT FIG. 1*c*, there are only *four* nuclear generations from the definitive archesporial cell to the mature sac. Since the first two of these nuclear divisions are followed by evanescent cell-walls, they may be regarded, as was pointed out above, as the equivalents of the first two cell-generations in TEXT FIG. 1*a*. That is, they are to be regarded as megaspore nuclei, and the mature embryo sac is the product of four megaspore nuclei, each megaspore nucleus dividing twice.

In the type illustrated by TEXT FIG. 1*d*, the definitive archesporial cell divides into an upper and a lower cell, of which the upper divides once more forming two potential megaspores, and the lower develops immediately, without the appearance of cell-walls, into an eight-nucleate embryo sac. Thus there are but *four* nuclear generations, from the definitive archesporial cell to the mature embryo sac, which is to be regarded as the product of the morphological equivalent of two megaspore nuclei.

In the type illustrated by TEXT FIG. 1*e*, there are *four* generations, one cell-generation and three nuclear generations, from th definitive archesporial cell to the mature embryo sac, which latter contains eight nuclei, and may be considered to be the product of the morphological equivalent of two megaspore nuclei, each dividing twice.

In the type illustrated by TEXT FIG. 1*f*, there are *four* generations, two cell-generations and two nuclear, from the definitive archesporial cell to the mature embryo sac. The sac here contains four nuclei and is clearly the product of one megaspore, which divides twice.

In the type illustrated by TEXT FIG. 1*g*, there are *three* nuclear generations, from the definitive archesporial cell to the mature embryo sac, which latter contains eight nuclei, and may be considered to be the product of the morphological equivalent of four megaspore nuclei, each dividing but once.

In the type illustrated by TEXT FIG. 1*h*, there are *three* generations, one cell-generation and two nuclear, between the definitive archesporial cell and the mature embryo sac, which latter contains four nuclei, and may be considered to be the product of the morphological equivalent of two megaspore nuclei, each dividing once.

In the type illustrated by TEXT FIG. 1*i*, the case is similar to

the preceding, the difference being that two evanescent cell-walls appear after the second division in the embryo sac, and that the lowest nucleus in the sac degenerates, so that the mature sac contains but three nuclei, which have arisen from the morphological equivalent of two megaspore nuclei.

If we accept this view of the phylogenetic sequence of the steps in the reduction of the development of sporogenous tissue, it is evident that *Peperomia*, as well as *Saururus*, *Ornithogalum*, and *Oenothera*, illustrates the first stage in the abbreviation of the development of megasporogenous tissue. The number of cell- or nuclear divisions from the definitive archesporial cell to the mature embryo sac has been reduced from five to four.

From the same point of view, *Piper*, as well as *Lilium*, *Cypripedium*, and *Podostemon*, illustrates the second stage in this reduction, where the number of cell or nuclear divisions from the definitive archesporial cell to the mature embryo sac has been reduced to three. This is the condition found by Yamanouchi (**80**) in *Fucus*, that is, the number of nuclear generations from the beginning of the reduction divisions to the mature egg is three.

As Miss Pace (**57**) has pointed out, if reduction should go one step further, we should have the condition present in the maturation of the animal egg. But no case showing reduction of the female sporogenous tissue to two cell-generations has been reported in plants.

It may be added that no unquestioned case of more than five cell and nuclear generations from definitive archesporial cell to mature embryo sac has been reported. Dessiatoff (**16**) reported a case of six cell-generations in *Euphorbia virgata*, but Modilewski (**52**) later got different results when working on the same species.

As has been frequently pointed out, there is much more variation in the development of embryo sacs than was formerly thought. Coulter & Chamberlain (**14**, p. 76, 77) call attention to the great variability in the family Liliaceae. The Podostemaceae, also, show considerable variation, as shown by Magnus (**44**). Sometimes the variability is very great in a single genus.

In the genus *Burmannia*, Ernst & Bernard (**22, 23**) found an interesting series of cases. In the species studied, the subepidermal primary archesporial cell becomes the definitive

archesporial cell without cutting off a parietal or tapetal cell. In *Burmannia Championii* this forms sometimes three, but usually four megaspores, and a typical eight-nucleate embryo sac develops from one of these, while the remaining two or three degenerate. In *B. candida* the definitive archesporial cell divides into two cells, the chalazal one giving rise to a typical eight-nucleate embryo sac, while the other degenerates. The division of the definitive archesporial cell is the heterotypic reduction division; therefore, the cell which gives rise to the embryo sac is the morphological equivalent of two megaspores. In *B. coelestis*, as a rule, the definitive archesporial cell develops directly into the embryo sac, without cutting off any non-functional megaspores. A typical eight-nucleate embryo sac is developed here from the morphological equivalent of four megaspores. It is interesting to note here that the end product in all three cases is a typical eight-nucleate sac, whether it is developed from one megaspore or from the morphological equivalent of two or of four megaspores.

In the genus *Euphorbia*, two species, *E. procera* and *E. palustris*, both investigated by Modilewski (**49, 51, 52**), have sixteen-nucleate embryo sacs, while at least thirteen other species of the same genus, investigated by the same author, have typical eight-nucleate embryo sacs. The latter condition was also found in *Ricinus*, *Phyllanthus*, *Securinega*, and *Croton*, four related genera belonging to the same family, the Euphorbiaceae.

Within a single species there is sometimes striking variation, as in *Epipactis pubescens* (Brown & Sharp, **5**), where usually the embryo sac arises from the innermost one of three megaspores, but in other cases four megaspores take part in the formation of the sac. The authors further state that there is some evidence that the embryo sac may at times be derived from two megaspores. In *Salix glaucophylla* (Chamberlain, **11**) there is even greater variation than in *Epipactis pubescens*.

That the origin of the embryo sac from the morphological equivalents of four megaspores as found in *Peperomia* is a derived condition rather than primitive, is further indicated by the following considerations:

(1) The vast majority of the embryo sacs of Angiosperms arise from a single megaspore, and the exceptions are not limited

to plants which for other reasons are known to be primitive. The sixteen-nucleate sacs, which have almost certainly arisen from four megaspores, are distributed among four families of dicotyledonous plants, the Piperaceae, the Haloragidaceae, the Penaeaceae, and the Euphorbiaceae, none of which except the first has been considered primitive.

The eight-nucleate embryo sacs, which have arisen from four megaspores or their morphological equivalents, are found in widely separated families of both monocotyledonous and dicotyledonous plants. They occur in *Typha* (Typhaceae) according to Schaffner (61), in *Lemna* (Lemnaceae) according to Caldwell (8), in *Lilium* (Liliaceae) according to Coulter (12), in *Epipactis* (Orchidaceae) according to Brown & Sharp (5), in *Piper* (Piperaceae) according to Johnson (32, 35), in *Salix* (Salicaceae) according to Chamberlain (11), in *Juglans* (Juglandaceae) according to Karsten (38), in *Avicennia* (Verbenaceae) according to Treub (77), and in *Aphyllon* (Orobanchaceae) according to Miss Smith (67).

While it may be doubted whether the embryo sac is the product of four megaspores or their morphological equivalents in all cases mentioned above, it certainly can not be doubted in cases like *Epipactis* (Brown & Sharp, 5) and *Smilacina* (McAllister, 45).

(2) In none of the heterosporous plants below the Angiosperms is the gametophyte known to be the product of the fusion of four germinating megaspores.

The endosperm nucleus of *Peperomia* in its origin from several nuclei shows a derived rather than a primitive condition, for nothing of this kind is found in other Angiosperms which are considered primitive, or in the heterosporous plants below the Angiosperms.

The endosperm of *Peperomia*, which is cellular from the start, exhibits in this condition a feature which is secondary rather than a characteristic that is primitive among Angiosperms.

The primary archesporial cell, which is single in *Peperomia*, represents a less primitive condition, according to Körnicke (40), than the multicellular archesporium which is found very much more commonly among the more primitive of the Dicotyledons than among the higher groups. The evidence for this view has also been briefly reviewed by Coulter & Chamberlain (14, p. 60).

Representatives of all four families of the order Piperales have been examined in an attempt to ascertain whether any species showed an intermediate stage between the embryo sac of *Peperomia* and that of the typical eight-nucleate embryo sac, and to see whether any feature of the development of the embryo sac confirmed the view that *Peperomia* is primitive.

Of the Piperaceae, besides the genus *Peperomia*, four species of *Piper* have been examined—three by Johnson (**32, 35**) and one by the writer and reported in this paper. All four have been shown to have eight-nucleate sacs, which develop directly from the definitive archesporial cell, no non-functional megaspores being formed. No other condition has been found in this genus. As was pointed out, the reduction in the number of generations, from the definitive archesporial cell to the mature embryo sac, has proceeded one step further in this genus than it has in the *Peperomia*.

Of the Saururaceae, species of *Saururus*, *Anemiopsis*, and *Houttuynia* have been examined by Johnson (**31, 33**), and *Houttuynia* by Shibata & Miyake (**66**), and it is found that one or more non-functional megaspores are cut off and that in all cases typical eight-nucleate embryo sacs are formed from single megaspores.

Of the Lacistemaceae, *Lacistema* (Johnson, **33**) shows a typical eight-nucleate embryo sac derived from a single megaspore.

Of the Chloranthaceae, *Hedyosmum* (Johnson, **33**) and *Chloranthus* (Armour, **1**) have been examined, each of which shows a typical eight-nucleate embryo sac which arises from a single megaspore.

A mode of origin and development of the embryo sac, which would confirm the idea that *Peperomia* is primitive, has not yet been found in any other genus of the order Piperales.

Finally, when we consider, (1) that the primary archesporial cell of *Peperomia* is single—a condition probably derived; (2) that the first four nuclei of the embryo sac are probably homologous with megaspores, certainly not a primitive feature; (3) that the peculiar origin of the endosperm nucleus here probably represents a derived condition; (4) that an endosperm which is cellular from the start can not be regarded as primitive; and (5) that none of the close relatives of *Peperomia* furnishes any indication, from the

development of the embryo sac, that the genus is primitive, we are inclined to accept the view first advanced by Johnson (30) and since confirmed by other workers (Brown, 4; Samuels, 59) that the peculiarities in origin and development of the embryo sac of *Peperomia* have been secondarily acquired.

SUMMARY

The primary archesporial cell is single and subepidermal in all species of *Peperomia* examined.

The nucleus of the definitive archesporial cell, or embryo sac mother-cell, goes into synapsis before its first division.

Evanescent cell-walls occur following the first and second nuclear divisions in the embryo sac in all six of the species of which the material was most nearly complete.

The mature sac contains sixteen nuclei, one of which functions as the egg nucleus, one as that of the single synergid, from six to nine others fuse to form the endosperm nucleus, and the remainder are individually cut off by cell-walls about the periphery of the sac and afterwards degenerate.

The endosperm is cellular from the start.

The embryo is undifferentiated externally except for a slight flattening on the micropylar side.

In *Piper tuberculatum* we have a typical eight-nucleate embryo sac, developed directly from the definitive archesporial cell, no degenerating megaspores being formed.

That the first four nuclei in the embryo sac of *Peperomia* are homologous with megaspore nuclei, seems extremely probable from the following facts: (1) they arise from a cell which with very little doubt may be considered a megaspore mother-cell; (2) they are arranged tetrahedrally; (3) the tetrad is complete in number; (4) the larger than usual number of nuclei in the mature sac is in harmony with this view; (5) the reduction of chromosomes occurs in the divisions which give rise to these four nuclei; (6) a resting stage follows the formation of these four nuclei; and (7) evanescent cell-walls frequently follow the first and second divisions in the embryo sac, but not the third.

In view of the following considerations: (1) that the primary archesporial cell of *Peperomia* is single—a condition probably

derived; (2) that the first four nuclei of the embryo sac are probably homologous with megaspores—certainly not a primitive feature; (3) that the peculiar origin of the endosperm nucleus here probably represents a derived condition; (4) that an endosperm which is cellular from the start cannot be regarded as primitive; and (5) that none of the close relatives of *Peperomia* furnishes any indication, from the development of the embryo sac, that the genus is primitive, the writer is inclined to believe that the peculiarities in origin and development of the embryo sac of *Peperomia* have been secondarily acquired.

Finally, I wish to thank those who have helped make this study possible. I am under obligation to Dr. Charles B. Davenport, Director of the Biological Laboratory of the Brooklyn Institute of Arts and Sciences, Cold Spring Harbor, Long Island, New York, for the use of a room in the Research Laboratory of that Institution in 1911; to Captain John Donnell Smith for the use of certain books from his library; to Dr. Casimir de Candolle for determining specimens of the plants studied; to Mrs. Bessie Wiley Fisher who carefully made the majority of my slides; and to Professor D. S. Johnson who collected a large portion of the material and to whom I am also greatly indebted for helpful criticism throughout the work.

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Explanation of plates 3–6

All figures are camera drawings except FIGS. 25 and 26, and all are from microtome sections except FIGS. 25, 26, and 36. The magnification given in the description of each figure is that actually shown by the figure as printed on the page.

FIGS. 1–18. *Peperomia reflexa*

FIG. 1. Longitudinal section of nucellus showing primary archesporial cell. × 670.

FIG. 2. Longitudinal section of ovule, showing definitive archesporial or embryo sac mother-cell, and parietal or tapetal cell. × 670.

FIG. 3. Longitudinal section of nucellus containing mature embryo sac mother-cell and two-layered tapetum. × 670.

FIG. 4. Longitudinal section of carpel showing subtending bract, nucellus, embryo sac mother-cell, integument, micropyle, stylar canal, and immature stigma. × 72.

FIG. 5. Longitudinal section of definitive archesporial cell, or embryo sac mother-cell, the nucleus showing synapsis. × 670.

FIG. 6. Nearly longitudinal section of a two-nucleate embryo sac showing evanescent cell-wall. × 670.

FIG. 7. Longitudinal section of a four-nucleate embryo sac showing tetrahedral arrangement of the nuclei. × 670.

FIG. 8. Longitudinal section of a four-nucleate embryo sac showing evanescent cell-wall. × 670.

FIG. 9. Longitudinal section of an eight-nucleate embryo sac. × 670.

FIG. 10. Longitudinal section of an embryo sac containing sixteen free nuclei. × 670.

FIG. 11. Longitudinal section of a mature embryo sac showing group of endosperm nuclei. × 670.

FIG. 12. Group of eight nuclei almost completely fused to form the endosperm nucleus (from transverse section of spike). × 670.

FIG. 13. Longitudinal section of an embryo sac showing egg, two peripheral nuclei, and two-celled endosperm. × 670.

FIG. 14. Longitudinal section of an embryo sac showing male nucleus within the egg, but not yet fused with the egg-nucleus, also the single synergid and the several celled endosperm. × 465.

FIG. 15. An embryo showing four cells in longitudinal section; endosperm several-celled. × 465.

FIG. 16. Longitudinal section of mature embryo and endosperm. × 300.

FIG. 17. Longitudinal section of a mature fruit showing how far it is sunk in the axis. × 50.

FIG. 18. Hydathode and hair from a transverse section of peduncle of spike. × 220.

FIGS. 19–27. *Peperomia verticillata*

FIG. 19. Transverse section of pollen-sac showing tapetum and tetrads of microspores. × 670.

FIG. 20. Longitudinal section of ovule showing primary archesporial cell; the integument just started. × 465.

FIG. 21. Longitudinal section of an embryo sac containing sixteen free nuclei. × 670.

FIG. 22. Longitudinal section of young carpel containing a lobed ovule. × 220.

FIG. 23. Longitudinal section of lobed ovule, older stage than preceding. × 50.

FIG. 24. Lateral exterior view of a reconstruction of a lobed ovule. × 80.

FIG. 25. Median longitudinal section of the preceding, showing integument and embryo sac of the fertile lobe. × 80.

FIG. 26. Transverse section of a lobed ovule, showing position of embryo sac in small fertile lobe. × 220.

FIG. 27. Longitudinal section of a deformed seed developed from a lobed ovule (somewhat diagrammatic). × 50.

FIGS. 28–34. *Peperomia scandens*

FIG. 28. Nearly longitudinal section of a two-nucleate embryo sac, showing the cell-plate, which is the beginning of the evanescent cell-wall. × 670.

FIG. 29. Transverse section of two-nucleate embryo sac showing evanescent cell-wall. × 670.

FIGS. 30, 31. Longitudinal sections of two-nucleate embryo-sacs showing evanescent cell-walls. × 670.

FIG. 32. Longitudinal section of a young carpel showing how far it is sunk in the axis. × 50.

FIG. 33. Longitudinal section of a mature fruit, showing how far it is sunk in the axis. × 50.

FIG. 34. Longitudinal section of the upper part of an embryo sac, showing the egg and the single synergid. × 670.

FIG. 35. *Peperomia metallica*

FIG. 35. Lateral view of an interrupted flower-spike, showing zone of small vegetative leaves. × 1.

FIG. 36. *Peperomia blanda*

FIG. 36. Longitudinal section of a four-nucleate embryo sac, showing evanescent cell-wall. × 670.

FIGS. 37–43. *Piper tuberculatum*

FIG. 37. Longitudinal section of young ovule, showing primary archesporial cell; integuments not yet started. × 670.

FIG. 38. Longitudinal section of a slightly older ovule, in which the primary archesporial cell has divided to the definitive archesporial cell and the parietal cell. × 670.

FIG. 39. Longitudinal section of slightly older ovule, showing definitive archesporial cell or embryo sac mother-cell; the parietal cell has divided forming tapetum four cells thick. × 670.

FIG. 40. Longitudinal section of nucellus, showing two-nucleate embryo sac. × 670.

FIG. 41. Same as preceding in outline with addition of integuments. × 220.

FIG. 42. Longitudinal section of four-nucleate embryo sac, showing the linear arrangement of the nuclei. × 670.

FIG. 43. Longitudinal section of eight-nucleate embryo sac, the two polar nuclei fusing to form the endosperm nucleus. × 670.

On the relationship between the number of ovules formed and the number of seeds developing in Cercis

J. Arthur Harris

(with three text figures)

I. Introductory Remarks

In an earlier paper* I have stated certain problems concerning the relationship between the number of ovules laid down and the capacity of the ovary for maturing its ovules into seeds, and have illustrated the methods which seem suitable to me for their solution by a series of data drawn from experimental cultures of *Phaseolus vulgaris*. The results of this first analysis of extensive series of data seem to render desirable the like treatment of other similar but quite distinct materials. The present paper is, therefore, devoted to the analysis of numerous data from a wild small-seeded arborescent legume, *Cercis canadensis*.

The study has been in progress since the autumn of 1905, when the first large series of countings was made. The results given in this paper were made ready for the press in January 1910, but the manuscript was laid aside in the hope that it would be possible to secure data which would show the relationship between the correlations discussed and the then just discovered selective mortality of ovaries. In this hope I have met with only disappointment, and it seems best to withold the materials no longer.

II. Materials

The materials here analyzed were collected in three series as follows:

A. A very large collection taken at Meramec Highlands, near St. Louis, Missouri; altogether 28,554 pods.

B. A collection from 22 trees in the neighborhood of Lawrence, Kansas; 2,200 pods.

* Harris, J. Arthur. On the relationship between the number of ovules formed and the capacity of the ovary for developing its ovules into seeds. Bull. Torrey Club 46: 447–455. Au 1913.

C. A collection from 26 trees near Sharpsburg, Athens County, Ohio; 3,900 pods.

The pods of *Cercis canadensis* are, like those of many other Leguminosae, somewhat unsatisfactory for investigations of fertility because of the difficulty of drawing a sharp line between ovules which fail to develop and those which form perfect seeds. It seems unfeasible, in the present state of our knowledge of these matters, to adopt more than the two categories, abortive ovules and matured seeds. In most cases, an observer will have little difficulty in determining to which class an individual ovule should be assigned. Nevertheless, we are dealing here with characters not perfectly discontinuous. This condition must always be borne in mind in considering the trustworthiness of our constants.

In counting, we considered as abortive ovules only those which had not developed at all, or only slightly, beyond the stage attained in the very young pod. Some of the seeds counted as matured were probably not well enough developed to be viable. Some of them were light and apparently blighted. The cause of this I do not know. The ovules failing to develop are not as easily made out in the mature pods of *Cercis* as they are in some other Leguminosæ; this increased somewhat the labor of counting.

III. DISCUSSION OF DATA

A. The Meramec Highlands Collections

The correlation between the number of ovules formed and the number of seeds developing in a first large sample of 6,000 pods, chiefly from a few (6 or 8) large trees growing closely together is shown in Table I. For comparison another 4,000 was gathered quite at random in the immediate neighborhood of the trees furnishing the first 6,000, but from a larger number (probably 25) of smaller trees: Table II gives the correlation surface.

The fundamental physical constants appear in Table III.

For the means the differences and probable errors of the difference of these two samples are

Ovules..... $+.1536 \pm .0137$
Seeds..... $-.0261 \pm .0166$

The ovules are about fifteen one-hundredths more numerous in the sample collected from the few large trees. This is certainly not a difference which would have been detected by other than biometric methods, and some might consider it neglible, but it is slightly over eleven times its probable error and so unquestionably

TABLE I

SEEDS

Ovules	1	2	3	4	5	6	7	
1	3	—	—	—	—	—	—	3
2	10	39	—	—	—	—	—	49
3	37	109	203	—	—	—	—	349
4	61	292	701	933	—	—	—	1,987
5	32	202	472	887	830	—	—	2,423
6	19	40	106	223	350	304	29	1,042
7	—	5	7	17	31	51	3	140
8	—	—	—	2	—	2		7
	162	687	1,489	2,062	1,211	357	32	6,000

TABLE II

SEEDS

Ovules	1	2	3	4	5	6	7	
1	4	—	—	—	—	—	—	4
2	14	89	—	—	—	—	—	103
3	29	147	254	—	—	—	—	430
4	34	160	435	678	—	—	—	1,307
5	17	105	207	485	568	—	—	1,382
6	3	19	46	122	210	277	—	677
7	—	3	2	11	17	26	36	95
8	—	—	—	—	1	1	—	2
	101	523	944	1,296	796	304	36	4,000

TABLE III

PHYSICAL CONSTANTS FOR RANDOM SAMPLES

Constants	6,000 Pods	4,000 Pods	10,000 Pods
Mean of ovules	4.7498 ± .0080	4.5952 ± .0112	4.6880 ± .0062
Standard deviation of ovules	.9274 ± .0057	1.0532 ± .0079	.9826 ± .0046
Coefficient of variation of ovules	19.5270	22.9215	20.9615
Mean of seeds	3.7786 ± .0102	3.8047 ± .0131	3.7891 ± .0081
Standard deviation of seeds	1.1781 ± .0072	1.2377 ± .0093	1.2024 ± .0057
Coefficient of variation of seeds	31.1792	32.5332	31.7337
Correlation, ovules and seeds	.5763 ± .0059	.6782 ± .0057	.6133 ± .0042

significant. No importance need to be attached to the difference for seeds developing, which is not twice its probable error.

The difference for the standard deviations and coefficients of variation are:

	Standard Deviation	Coefficient of Variation
Ovules	$-.1258 \pm .0097$	-3.395
Seeds	$-.0596 \pm .0117$	-1.354

The difference in S.D. for ovules is nearly 13 times its probable error and for seeds about 5 times its probable error. Both are clearly significant.

The difference for the coefficient of correlation is

$$r_s \quad -.1199 \pm .0082,$$

a difference 13.5 times its probable error and undoubtedly significant.

It appears, therefore, that our samples are sensibly differentiated from each other in type, variability and correlation. This fact is sufficient ground for considering their correlations independently.

The significance of the coefficient of correlation depends upon linearity of regression. Using the familar equation for the regression straight line

$$s = \left(\bar{s} - r \frac{\sigma s}{\sigma o} \bar{o} \right) r \frac{\sigma s}{\sigma o} o$$

I find

For first 6,000	$s = .3554 + .7207\, o$
For additional 4,000	$s = .1423 + .7970\, o$
For first 10,000	$s = .2712 + .7504\, o$

The closeness of agreement of the observed means and those given by the equation is evident from Table IV where the two are compared. If the two extreme variates, where the numbers of observations are so small that little weight is to be attached to them, be omitted, there is only a single case out of the eighteen where the deviation of the observed from the theoretical mean reaches thirteen one-hundredths of a seed.

The average (weighted) deviations (disregarding signs) of the

TABLE IV

DEVIATION OF OBSERVED MEANS OF ARRAYS FROM THEORETICAL MEANS AS CALCULATED FROM THE REGRESSION STRAIGHT LINES

Ovules per Pod	First 6,000 Pods				Additional 4,000 Pods				First 10,000 Pods			
	N	Observed Mean Seeds	Calculated Mean Seeds	Difference	*N*	Observed Mean Seeds	Calculated Mean Seeds	Difference	*N*	Observed Mean Seeds	Calculated Mean Seeds	Difference
1	3	1.000	1.076	+.076	4	1.000	.939	− .061	7	1.000	1.022	+.023
2	49	1.796	1.797	+.001	103	1.864	1.736	+ .128	152	1.842	1.772	−.070
3	349	2.476	2.517	+.042	430	2.523	2.533	+ .010	779	2.502	2.522	+.020
4	1,987	3.261	3.238	−.023	1,307	3.344	3.330	− .014	3,294	3.294	3.273	−.021
5	2,423	3.941	3.959	+.018	1,382	4.072	4.127	+ .055	3,805	3.989	4.023	+.034
6	1,042	4.686	4.680	−.006	677	4.991	4.924	− .067	1,719	4.806	4.774	−.033
7	140	5.450	5.400	−.050	95	5.779	5.721	− .058	235	5.583	5.524	+.059
8	7	5.857	6.121	+.264	2	5.550	6.518	+1.018	9	5.778	6.274	+.497

empirical from the theoretical means is .0198 for the first 6,000, .0411 for the additional 4,000, and .0302 for the total 10,000 pods. The fit is also shown graphically for the 6,000 pod lot in FIG. 1.

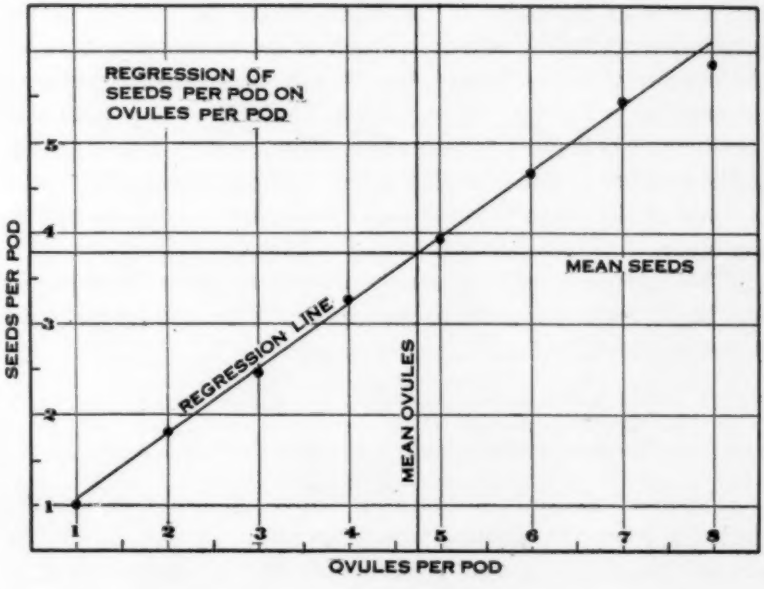

FIG. 1

For the 6,000 nd the 10,000 lots, I have calculated η as well as r. I find

Constant	Series of 6,000 Pods	Series of 10,000 Pods
Coefficient of correlation, r	$.5673 \pm .0059$	$.6133 \pm .0042$
Correlation ratio, η	$.5677 \pm .0059$	$.6140 \pm .0038$
Difference, $\eta - r$	.00035	.00066
$\eta^2 - r^2 = \zeta$	.00040	.00081

Note the exceedingly small differences between r and η. For a scientific test of linearity, we have recourse to the constant ζ as suggested by Blakeman,* *i. e.*:

$$\frac{1\sqrt{N}}{.67449} \cdot \tfrac{1}{2}\sqrt{\zeta} < 2.5$$

which gives

For 6,000 pods ..... $\zeta/E_\zeta = 1.144$
For 10,000 pods ..... $\xi/E_\xi = 2.110$

Hence regression may be considered linear within the limits of the probable errors of random sampling.

The reason so much stress has been laid upon the question of the nature of regression is two-fold. First, the validity of the correlation coefficient as a description of the relationship between the number of ovules formed and the number of seeds developing depends upon linearity of regression. Second, it is a matter of considerable biological importance to know that the rate of change in the number of seeds developing per pod remains constant from one end of the range of variation of number of ovules per pod to the other.

The coefficient which measures the relationships between the number of ovules per pod and the capacity of the pod for maturing its seeds is not r_{os} but r_{oz}. The results are:

For the first 6,000 ..... $r_{oz} = -.0714 \pm .0087$
For the additional 4,000 ..... $r_{oz} = -.0358 \pm .0106$
For the whole 10,000 ..... $r_{oz} = -.0597 \pm .0067$

The first and third constants are clearly significant statistically deviating from 0 by about 8 or 9 times their probable errors: the second constant may also be significant but it differs from 0 by only about 3.5 times its probable error. They indicate that the pods with the larger number of ovules are not as capable of matur-

* Biometrika 4: 332–350. 1905.

ing their ovules into seeds as those which do not produce so many, but that the relationship is a very slight one.

The differences between two random samples taken so closely together and the very low correlation makes one cautious in accepting our constants as biologically significant for *Cercis* as a species, or even for *Cercis* as a race growing at Meramec Highlands. Under the circumstances the only thing to be done is to collect wider series of data.

The collection of this additional material was carried out from two standpoints; first that of widening the sources of pods in number of trees and variety of habitats, second, that of securing greater homogeneity in the series of pods upon which individual constants are based by taking them all from individual trees. The discussion of the results of analysis of data for the individual trees must be reserved for a later contribution. In addition to the general samples just described from Meramec Highlands, smaller lots were taken from about 125 trees. These can be added to the 10,000 pods already discussed.

TABLE V

SEEDS

Ovules	1	2	3	4	5	6	7	8	
1	7	—	—	—	—	—	—	—	7
2	67	281	—	—	—	—	—	—	348
3	190	837	1,407	—	—	—	—	—	2,434
4	236	1,264	3,536	4,582	—	—	—	—	9,618
5	100	620	1,691	3,630	3,955	—	—	—	9,996
6	46	142	444	1,064	1,787	1,806	—	—	5,289
7	2	21	42	88	180	261	232	—	826
8	—	1	—	4	10	6	10	5	36
	648	3,166	7,120	9,368	5,932	2,073	242	5	28,554

Consider now the total material, amounting to 28,554 pods, from Meramec Highlands. The data appear in Table V. The constants are:

$$A_o = 4.7020 \pm .0040, \qquad A_s = 3.8399 \pm .0048,$$
$$\sigma_o = 1.0074 \pm .0028, \qquad \sigma_s = 1.2036 \pm .0034,$$
$$V_o = 21.425, \qquad V_s = 31.3452.$$
$$r_{os} = .6482 \pm .0023, \qquad r_{oz} = -.0463 \pm .0040.$$

The equation to the regression straight line is

$$s = .1983 + .7745\, o.$$

The means and the fitted line are seen in FIG. 2. Except for the final class, 8, the agreement of the predicted and the observed means is excellent, so close, indeed, that it is impossible to represent it graphically on a diagram of the size to be published on our page.

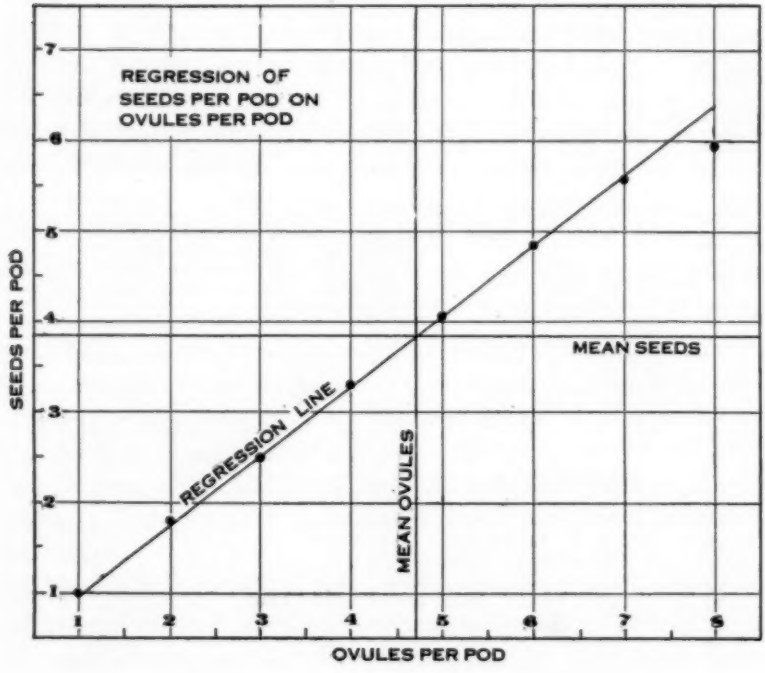

FIG. 2

To test more critically the linearity of regression, I determined the correlation ratio, η, and compared it with the coefficient of correlation r. I find

$$\eta = .648443,$$
$$r = .648226,$$
$$\eta - r = .000217,$$

a very close agreement indeed.

Applying Blakeman's test* and using this time his more exact formula,

$$\frac{\zeta}{E_\zeta} = \frac{\sqrt{N}}{.67449} \cdot \tfrac{1}{2}\sqrt{\zeta} \cdot \frac{1}{\sqrt{1 + (1-\eta^2)^2 - (1-r^2)^2}}$$

I find

$$\eta^2 - r^2, \ = \zeta, \ = .000281,$$

which gives

$$\zeta/E_\zeta = 2.101.$$

As far as one can state with certainity, therefore, the deviations of the observed means from the straight line due to the equation may be due to nothing more than the probable errors of random sampling. Comparing this diagram with those for other series of *Cercis*, I think it not unlikely that the falling off in the mean number of seeds for the pods with 8 ovules is biologically significant.

Here again, the sign of the correlation, r_{oz}, is negative and its value very small. However $r_{oz}/Er_{oz} = 11.63$, and perhaps it is a significant relationship.

It may have occurred to the reader that the negative relationship between the number of ovules per pod and the capacity of the pods for maturing their seeds may be due to some purely mathematical difficulty in dealing with the biological data—perhaps to some approximation in the formula.

To reassure those who may be skeptical on this ground, I have actually determined the deviation of each number of seeds per pod from the probable number which would have occurred if fecundity had been the same throughout all the population and have determined the correlation between these deviations and the number of ovules per pod.

In calculating the probable number of seeds for each pod the total seeds matured for all the pods was divided by the total ovules formed to get P, the probability of any ovule in the entire population—i. e., irrespective of the number of ovules in the pod in which it occurred—developing into a seed. This was

$$P = 109{,}644/134{,}261 = .816{,}648.$$

* Biometrika 4: 350. 1905.

To obtain the probable number of seeds developing in any class of pods the number of ovules is multiplied by P.

In carrying out the arithmetic of the calculation of r_{os} by the "brute force" method all the deviations were written down to six decimal places. The values of r_{os} are:

Calculated by formula	−.046315
Calculated by "brute force"	−.046311
Difference	.000004

Comments are superfluous.

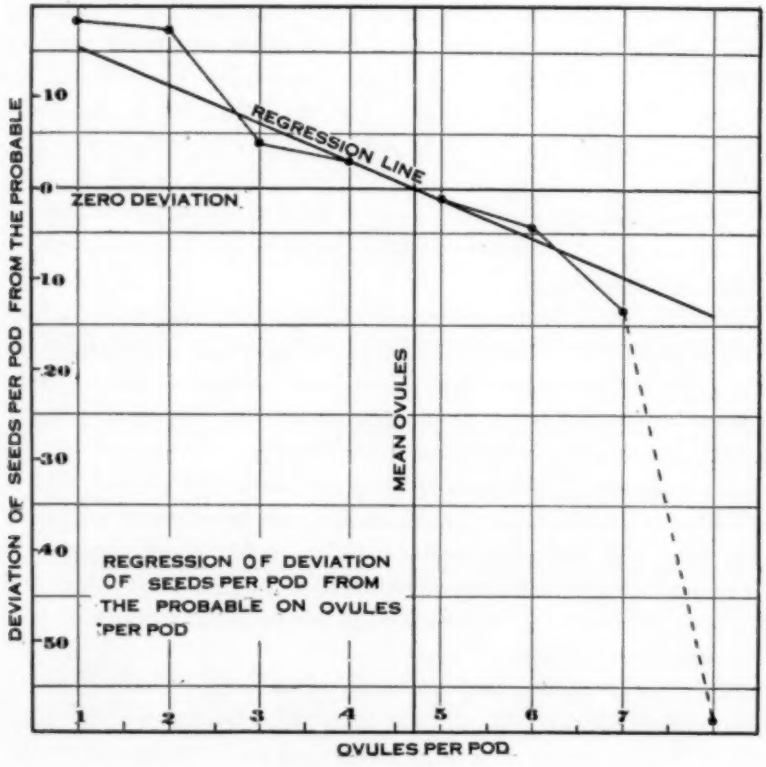

FIG. 3

Having actually obtained the deviations of the fertility of the individual pods from the probable fertility, it is easy to calculate the mean deviation for the arrays associated with different

numbers of ovules per pod. The standard deviation may also be computed for the entire material. The slope of the regression line is

$$z = .19833 - .04217\ o.$$

The slope of this line and the empirical mean deviations are shown in FIG. 3.

It thus appears that while the relationship is an exceedingly slight one, in all the adequately large series of material from Meramec Highlands the capacity of the pods for maturing their seeds decreases as the number of ovules per pod increases.

B. Analysis of The Data from the Vicinity of Lawrence, Kansas

I have to thank my father, Mr. J. T. Harris, for the collection of a series of 100 pods each from 22 trees in the neighborhood of Lawrence, Kansas. All the trees grew in the same small field.

The correlation between the number of ovules per pod and the number of seeds developing per pod for the total material from the 22 individuals is set forth in Table VI. The results are:

$$A_o = 4.916 \pm .013, \qquad A_s = 4.116 \pm .015,$$
$$\sigma_o = .925 \pm .009, \qquad \sigma_s = 1.030 \pm .010,$$
$$V_o = 18.82, \qquad V_s = 25.03,$$
$$r_{os} = .603 \pm .009, \qquad r_{oz} = -.183 \pm .014.$$

For the lumped conclusions, where $N = 2{,}200$, I find:

$$r_{oz}/Er_{oz} = 13.19.$$

C. Analysis of the Data from the Vicinity of Sharpsburg, Ohio

I am indebted to my grandfather, Mr. J. W. Harris, for the collection of 150 pods each from a series of 26 trees growing in the neighborhood of Sharpsburg, Athens Co., Ohio.

Calculating from the grand total of nearly 4,000 pods summarized in Table VII, I find:

$$A_o = 5.493 \pm .011, \qquad A_s = 3.944 \pm .016,$$
$$\sigma_o = .983 \pm .008, \qquad \sigma_s = 1.453 \pm .011,$$
$$V_o = 17.89, \qquad V_s = 36.83,$$
$$r_{os} = .455 \pm .009, \qquad r_{oz} = -.034 \pm .011.$$

Here $r_{os}/Er_{os} = 3.15$. Possibly this value is statistically significant, but considering its extremely small magnitude I think one should be cautious in attaching any biological significance to it.

TABLE VI

SEEDS

Ovules	1	2	3	4	5	6	7	
2	—	2	—	—	—	—	—	2
3	1	24	65	—	—	—	—	90
4	2	47	234	384	—	—	—	667
5	—	27	127	350	361	—	—	865
6	—	12	44	112	174	143	—	485
7	—	—	4	11	29	27	19	90
8	—	—	—	—	1	—	—	1
	3	112	474	857	565	170	19	2,200

TABLE VII

SEEDS

Ovules	0	1	2	3	4	5	6	7	8	9	
3	1	2	23	23	—	—	—	—	—	—	49
4	18	27	106	194	162	—	—	—	—	—	507
5	36	41	182	320	504	381	—	—	—	—	1,464
6	26	17	86	212	295	420	265	—	—	—	1,321
7	5	4	25	41	95	110	120	74	—	—	474
8	1	1	2	8	9	12	24	18	6	—	81
9	—	—	—	—	1	—	1	—	1	1	4
	87	92	424	798	1,066	923	410	92	7	1	3,900

D. Comparison of Constants from Three Series of Cercis

A detailed comparison of the characters of red bud from various regions of the United States or from different habitats falls outside the scope of this paper. I will, however, lay the results from the total materials of the three side by side for a casual comparison in Table VIII.

It is clear without further arithmetic that many of these constants differ significantly from series to series, that is to say, the difference between them is several times as large as can be attributed to the errors of sampling from a homogeneous population. This fact does not, however, necessarily indicate that the three series are "genetically," "racially" or "genotypically" distinct. Each general collection is composed of a (relatively) small number of trees. These individuals are, as will be shown later, differenti-

ated in number of ovules and number of seeds per pod, and probably in the variability and correlation of these two characters. Since the general samples are made from a relatively small number of these individual trees some differences between collections might arise through the errors of sampling in the selection of individuals.

TABLE VIII

COMPARISON OF THREE SERIES OF *Cercis*

	Missouri Series	Kansas Series	Ohio Series
Total individuals	More than 123	22	26
Total pods	28,554	2200	3900
OVULES			
Mean	4.702 ± .004	4.916 ± .013	5.493 ± .011
Standard deviation	1.007 ± .003	.925 ± .009	.983 ± .008
Coefficient of variation	21.43	18.82	17.89
SEEDS			
Mean	3.840 ± .005	4.116 ± .015	3.944 ± .016
Standard deviation	1.204 ± .003	1.030 ± .010	1.453 ± .011
Coefficient of variation	31.35	25.03	36.83
OVULES AND SEEDS			
Correlation, r_{os}	.648 ± .002	.603 ± .009	.455 ± .009
Correlation, r_{oz}	−.046 ± .004	−.183 ± .014	−.034 ± .011
Coefficient of fecundity	.8166	.8373	.7180

Again, no account whatever can be taken of environmental conditions, either edaphic or meterological.

With two such factors, which may to some extent tend to bring about differences in the constants of the series dealt with, it has seemed to me rather surprising that the physical constants for ovules and seeds do not differ more widely than they do.

The coefficients of correlation, r, differ considerably; but two factors influencing this constant must not be forgotten. First, heterogeneity, due to the mixing of the pods from a large number of individuals, would tend to raise the value for the Missouri series. This appears very clearly in a comparison of the mean for the 60 individual constants from trees with 100 pods each and the constant for the 28,000 and more pods in the lumped sample. The former is .599, the latter .648. Second, the coefficients of fecundity show that the three series differ very materially in the percentage of ovules developing into seeds. The lowest value of the coefficient of correlation for ovules formed and seeds maturing (in the Ohio series) is associated with the lowest value of the coefficient of fecundity.

Finally, perhaps the most important point to be gathered from

this table is that in all three series r_{oz} is negative and of a very low order, but quite possibly significant even in the Ohio series.

E. Summary and Discussion

The foregoing pages embody the results of an attempt to ascertain the relationship between the number of ovules per pod and the capacity of the pod for maturing its ovules into seeds in the leguminous plant *Cercis canadensis*. The methods of analysis are those of an earlier paper on *Phaseolus*. The data in hand lead to the following conclusions:

The correlations for number of ovules formed and number of seeds developing per pod, r_{os}, have always been found positive and of a moderate, considerable or even high intensity.

Regression of number of seeds on number of ovules per pod is sensibly linear in a population of pods from many individual trees. Possibly, however, there is a departure from linearity in the pods with eight ovules; in my largest series there are only 36 of these pods out of a total of 28,554, and this number is too small to be given great importance.

The significance of the linearity of regression is two-fold. Statistically, it justifies describing the interdependence between the number of ovules formed and the number of seeds maturing by the coefficient of correlation. Biologically, it shows that the rate of increase in number of seeds developing per pod remains the same as we pass from pods with the lowest to pods with the highest numbers of ovules.

Wherever large series of pod have been examined, the correlation between the number of ovules per pod and the capacity of the pods for maturing their seeds, r_{oz}, has a negative sign and a low, usually a very low, magnitude. For every large series examined the value of r_{oz} has been over 2.5 times its probable error. These evidences can leave little doubt of the existence of a slight negative relationship between the number of ovules formed and the capacity of the pod for maturing its ovules into seeds, the pods with the larger number of ovules producing relatively fewer seeds.

In a subsequent paper, these conclusions will be tested upon the more homogeneous collections of pods from individual trees. Until then further discussion may be reserved.

COLD SPRING HARBOR, NEW YORK

INDEX TO AMERICAN BOTANICAL LITERATURE

1913–1914

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

Reviews, and papers that relate exclusively to forestry, agriculture, horticulture, manufactured products of vegetable origin, or laboratory methods are not included, and no attempt is made to index the literature of bacteriology. An occasional exception is made in favor of some paper appearing in an American periodical which is devoted wholly to botany. Reprints are not mentioned unless they differ from the original in some important particular. If users of the Index will call the attention of the editor to errors or omissions, their kindness will be appreciated.

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